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Differences in bird community structure between riparian and upland zones in a New Guinean rainforest

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Abstract. Riparian forests serve as important habitats that enhance diversity of bird species and perform crucial ecosystem functions in tropical forest landscapes. We compared the community structure (represented by functional trait composition) and diversity (represented by Shannon index) of birds in riparian and upland zones in a semi-continuous primary rainforest in Papua New Guinea. Distance sampling was applied to provide unbiased abundance estimates. Bird community structure was examined by principal coordinate analysis of neighbour matrices (PCNM) in the Canoco 5 program. Analysis of diversity was performed using mixed-effects linear models in R 3.5.1. Species diversity was marginally higher in riparian zones ($P = 0.065$). Community structure differed significantly in riparian and upland zones ($P = 0.008$). Invertivorous and omnivorous birds preferred riparian habitats but frugivorous and nectivorous birds avoided riparian zones. Birds in riparian zones were characterised by preferences for high-density forest interior but birds in upland areas mostly occupied exposed canopy layers. Beak dimensions were greater in riparian zones but body mass, and lengths of wing and tarsus were greater in upland zones. Species found in riparian zones had greater geographical ranges than those in upland zones. Our results highlight the adaptability of a rainforest bird community to natural disturbances characterised by localised river flooding and riverbank erosion. For example, small invertivorous and omnivorous birds can navigate disturbed vegetation and exploit river-associated invertebrate food supply while moving to alternative food sources during intensive flooding. On the other hand, large frugivorous and nectarivorous birds are mostly sedentary and require an intact canopy layer for foraging, responding poorly to changes in vegetation structure. By moving beyond species-level relationships when examining bird community structure, we were able to better interpret and connect our findings with other studies on bird communities in tropical rainforest.

Introduction

Bird communities are often used as study models in tropical ecology, as they respond quickly to landscape modification (Helms *et al*. 2018), are a relatively easy group to monitor (Gardali *et al*. 2006) and are recognised as reliable indicators of changes in vegetation structure (Da Silva & Vickery 2002). Anthropogenic disturbances and large-scale landscape modifications are responsible for the most drastic structural changes in rainforest landscape (Fahrig 2003; Sodhi *et al*. 2004) but natural disturbance regimes continue to play an integral role in ecosystem functioning. Natural disturbance dynamics are facilitated by periodic events such as flooding, landslides or bushfire (Melick & Ashton 1991). Different types of disturbances are common in tropical rainforests (Maicher *et al*. 2020) and significantly increase habitat heterogeneity (Kamga *et al*. 2022). Flooding and riverbank erosion often lead to breaks in canopy continuity and changes in vegetation structure (Salo *et al*. 1986). The natural disturbance regimes of riparian areas directly influence the availability of resources for birds (Uesugi & Murakami 2007) and facilitate seed dispersal (Richter & Stromberg 2005). Riparian bird communities can be highly diverse because of seasonal variation in water flow (Remsen & Parker 1983) and safe nesting opportunities in patches of land isolated by water (Ocampo & Londoño 2015). Riparian sites provide refuge for bird species in fragmented rainforests (Sekercioglu *et al*. 2015), provide water and food sources during drought for birds from the surrounding areas (Hinojosa-Huerta *et al.* 2013) and generally retain valuable communities (Mitchell *et al*. 2018), representing desirable areas for study of bird communities.

Because of the character of examined disturbances, a rainforest study site unaffected by large-scale fragmentation from commercial logging or road construction was selected. The forests of Papua New Guinea have been partially damaged by conversion into agricultural landscapes but still largely retain their continuity (Shearman *et al*. 2009). One of the more well-preserved regions is the Wanang Conservation Area, ~11,000 hectares in size. Natural disturbances within this area are caused by several small rivers creating forest edges by eroding the riverbanks, and anthropogenic disturbances are restricted to occasional hunting and selective timber gathering. The primary forest here is characterised by high bird diversity (>500 bird species: Anderson-Teixeira *et al.* 2015). Bird community structure and its response to environmental effects have been investigated in several studies in the region. Bell (1984) examined foraging ecology of birds and discussed the organisation of different trophic niches in lowland rainforest near Port Moresby, Papua New Guinea. Trophic niches of birds in the Wanang Conservation Area were examined by Chmel *et al*. (2016) as part of a study on vertical bird community stratification. Another study, by Tvardíková (2010), examined effects of moderate forest fragmentation and found that insectivorous and frugivorous birds were highly sensitive to disturbances. Bird functional traits describing stratification and trophic niches were examined as part of an investigation into the effect of forest fragmentation on bird communities by Sam *et al.* (2014), and a second study examining bird diet along an elevational gradient was performed by Sam *et al.* (2017).

These studies organised bird species into trophic niches or foraging strata to investigate bird community structure. Functional traits are frequently used to comprehensively assess bird response to environmental factors and are applicable to bird communities across different regions and ecosystems (Vandewalle *et al*. 2010; Newbold *et al*. 2014; Batisteli *et al*. 2018; Bender *et al*. 2019). By moving beyond species-level community assessment, functional traits lead to better understanding of ecosystem structure and function (Cadotte *et al*. 2011; Cernansky 2017).

Numerous studies have compared bird communities in riparian habitats with those of upland areas (Bub *et al*. 2004; Rodewald & Matthews 2005; Palmer & Bennett 2006; Lehmkuhl *et al*. 2007). However, this comparison has not yet been made in Papua New Guinea. Also, comparisons of bird communities between large, mostly unconnected landscapes are often influenced by confounding factors (such as habitat isolation and edge effect: Ewers & Didham 2006) that distort bird distribution patterns. To avoid these confounding effects, our study was performed on a smaller spatial scale than these previous studies and was located entirely within a single semi-continuous primary rainforest area. Within this area, we aimed to determine whether the bird community exhibits similar patterns of altered community structure and increased bird diversity as reported by other researchers in riparian rainforests. To do this, we proposed these hypotheses: (1) bird diversity will be significantly increased in riparian zones and (2) community structure will differ significantly in riparian and upland areas. To test these hypotheses, we used a newly introduced functional trait dataset that had not yet been applied to examining riparian rainforest bird communities (Tobias *et al.* 2022), and employed multivariate analyses while controlling for the effect of spatial autocorrelation.

Methods

Collection of data

The fieldwork took place in tropical lowland forest close to the Swire Research Station (5°14′S, 145°05′E; 134 m above sea level) in the Wanang Conservation Area within the Madang Province of Papua New Guinea (Figure 1). Our study site was situated within >10,000 ha of primary vegetation with small secondary-growth sites, resulting from riverbank erosion and flooding along several small rivers (Figure 1). The study area consisted of smaller valleys (~300 m wide) created by flowing water, surrounded by hills (≤100 m high) covered in dense primary rainforest (Figure 2). The vegetation in the valleys is subject to regular flooding related to heavy seasonal rainfall of >4000 mm (McAlpine *et al.* 1983), as well as riverbank erosion (Figure 2). The distinction between riparian and upland forest was therefore based on whether the vegetation was subject to river-related disturbances in the valleys or whether it was located on elevated ground in the surrounding upland areas. To survey the bird community, we established two transects: the first was within 50 m of the riverbanks in riparian vegetation of the valleys, and the second was on elevated ground at least 300 m away from any streams or rivers, with the elevation range of the upland transect being within 100–200 m above sea level (Figure 1). Point-counts were employed as the core method for collection of field data, as they can easily be adjusted for usage in rainforest interior (Volpato *et al*. 2009; Martin *et al*. 2017; Mulvaney & Cherry 2020). On each transect, 10 point-counts were made, at least 200 m from each other to avoid overlapping of bird communities from neighbouring points (Figure 1).

Data were collected over an 8-day period from 7 to 14 August 2019 each day from 0600 to 0930 h. All points were surveyed four times by two observers together: (1) MK, a local in the Wanang region with substantial experience of bird sampling in the field as part of work for other researchers in the region (e.g. Sam *et al.* 2017), who recorded all individual birds sighted or heard within a distance of 50 m to assess the abundance of each species and (2) KK, a non-native with limited experience of bird identification, thus always accompanying MK, who estimated the distance of individual birds from the observer using a laser rangefinder, using five distance categories (0–10, 11–20, 21–30, 31–40 and 41–50 m). Birds were sampled at each point for a duration of 15 minutes. Data were collected during similar weather conditions with absence of precipitation. We used the latest (13.1) version of the IOC World Bird List (Gill *et al.* 2023) as reference authority for bird species nomenclature.

The maximal abundances of each species for each point during the four survey periods were adjusted by a distance sampling method as recommended by Marques *et al*. (2007). The process included using original abundances as input data to fit detection functions for separate species and distance categories using the function abundEstim, package RDistance (McDonald *et al*. 2015; Miller *et al*. 2017) in R 3.5.1 software (R Core Team 2019). The data import and analysis process were adapted from a detailed step-by-step tutorial by Carlisle & McDonald (2015). Using distance sampling allowed us to avoid incorrect conclusions regarding habitat relationships that may result from using non-adjusted abundances (Thompson 2002; Hill & Hamer 2004). Bird abundances adjusted by distance sampling were used to establish response variables for multivariate analysis. First, a data table containing estimated maximal bird abundance (after correcting for distance-based detection biases) of each species on each study plot over all visits was established. Available functional trait information was also employed in community structure analyses in this study. A data table of functional trait values of each species at our study site was derived from the AVONET database, as introduced by Tobias *et al*. (2022). In summary, we used four traits referring to life history (exposure of habitat, trophic niche, primary lifestyle and geographical range) and seven morphological traits (beak length, width and depth, lengths of tarsus, wing and tail, and body mass). Trophic niche split up birds into five categories: vertivores (species whose diet is composed mainly of vertebrates), invertivores (invertebrates), granivores (seeds), frugivores (fruits), nectarivores (nectar) and omnivores (diet highly variable). Primary lifestyles were insessorial (for birds that spent most of their time perching), aquatic (most time spent near water bodies), aerial (in flight), terrestrial (on the ground) and generalist (highly variable, combining other lifestyles). The list and more detailed explanations of employed functional traits are in Appendices 1–3. These data tables were used

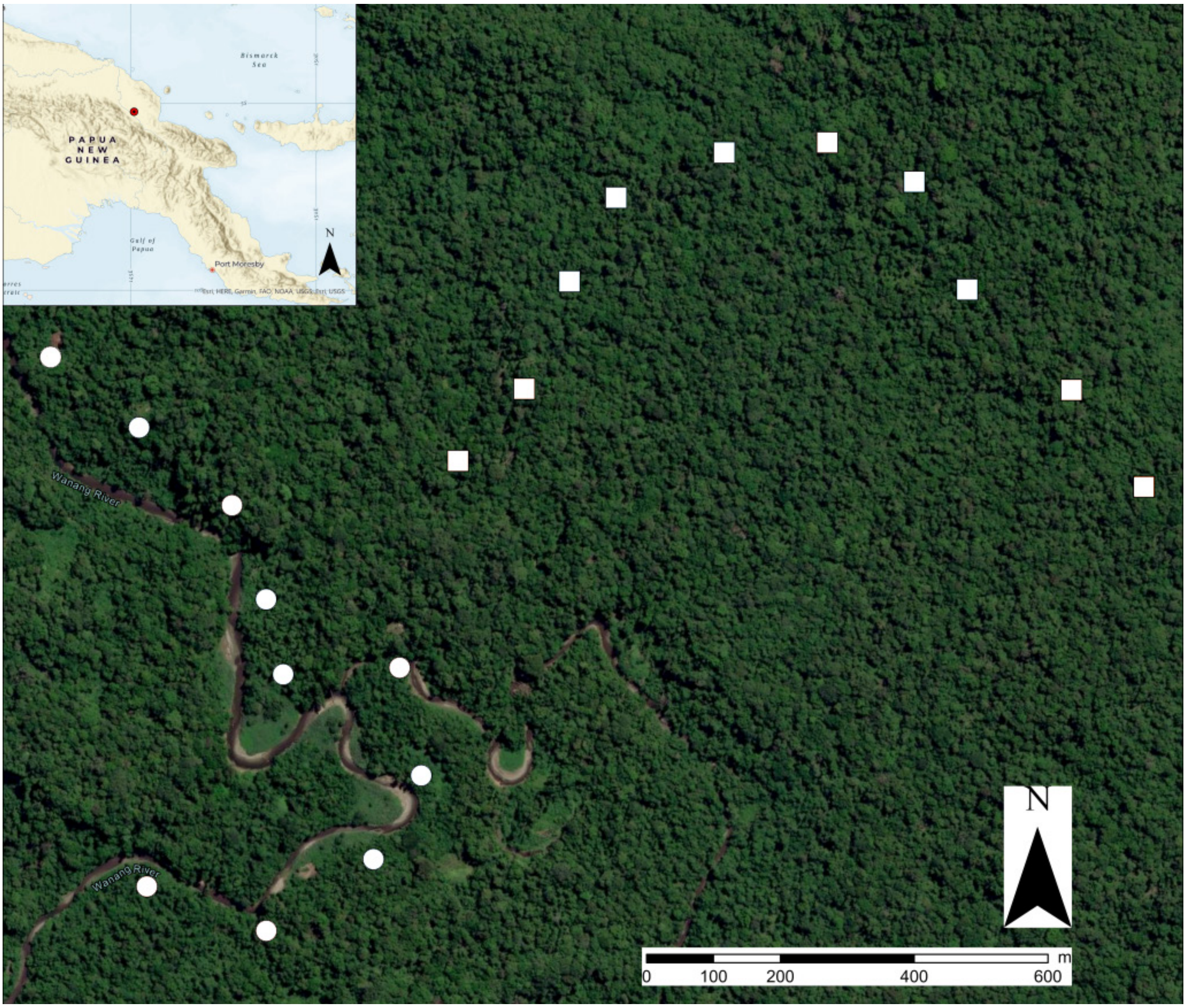

Figure 1. Aerial map of the study site and surrounding area. Sampling points where point-counts were performed are highlighted. White circles represent riparian zone points, and white squares represent points in upland zone. The location of the study site in Papua New Guinea is highlighted by the red circle in the inset map. Image created using ArcGIS Pro basemap service (Esri 2020)

to calculate a community weighted means (CWM) table where each study plot was characterised by a weighted average value of each functional trait. This method was recommended for examining community functional trait response to environmental characteristics by Kleyer *et al*. (2012) and Šmilauer & Lepš (2014).

Statistical analyses

We used a multivariate analysis to calculate the effect of river presence that represented the distinction between riparian and upland zones (primary predictor) on bird community structure. The data table containing community weighted means (CWM) of functional traits was used to represent community structure. We used variance partitioning by principal coordinate analysis of neighbour matrices (PCNM) in Canoco 5 software (Šmilauer & Lepš 2014) that was recommended by Marrot *et al*. (2015). This method enabled us to separate the effect of spatial autocorrelation (spatial predictors) from the effect of primary predictors (Legendre & Legendre 2012). It is suitable for calculating inter-correlated variables since all the variables enter the process simultaneously. Both analyses included nine steps: (1) primary predictor test (preliminary test of the overall effect of primary predictors on the dataset), (2) primary predictor testing by partial redundancy analysis (RDA) based on partial Monte Carlo permutation tests (n = 499 permutations), (3) principal coordinate analysis (PCoA) based on Euclidean distances (finding the main space predictors based on GPS coordinates), (4) PCNM for all predictors (preliminary test of the overall effect of space predictors on the dataset), (5) PCNM selection (the choice of space predictors based on coordinates using forward selection and partial Monte Carlo permutation tests), (6) spatial effects analysis (assessing the amount of variability explained by space predictors), (7) primary predictor effects analysis (assessing the amount of variability explained by primary predictors), (8) joint effects analysis (assessing the amount of variability explained by both predictor types) and (9) removal of spatial effects (Šmilauer & Lepš 2014).

Figure 2. Representative habitat types from this survey: riparian forest and upland forest. Riparian forest was characterised by development of secondary vegetation because of river-related disturbances, and upland forest consisted of dense primary vegetation with almost full canopy coverage. Photos: Jan Lenc

Maximum abundance of each species after adjustment by the distance sampling method at each count-point over all visits was used to calculate Shannon diversity indices (Shannon & Weaver 1949) on all 20 sampling points for each separate distance category (*n* = 5). The effect of river presence (representing the distinction between riparian and upland zones) on Shannon index values at observational points was calculated using a mixed-effect linear model (Gałecki & Burzykowski 2013), using function lmer, package lme4 (Bates *et al.* 2014) in R 3.5.1 software. Although imperfect detection of bird individuals was considered by distance sampling, another confounding factor during analysis of species diversity was the effect of interaction between distance from observer and habitat type. To remove this confounding factor, distance from observer was used as a random effect covariate. The mixed-effect linear model was used because it provides a better, more robust framework for analysing datasets that include covariates than other methods (Boisgontier & Cheval 2016).

Results

Community overview

We recorded 857 individual birds from 83 species and from 29 families (derived from maximum counts over all four visits: Appendix 1). The most abundant species was the Northern Variable Pitohui *Pitohui kirhocephalus* (*n* of recorded individuals = 75). Other abundant species were the Sepik-Ramu Shrike-thrush *Colluricincla tappenbecki* (*n* = 43) and Black-sided Robin *Poecilodryas hypoleuca* (*n* = 37). The majority of species at our study site lived within the understorey and high-density midstorey (*n* = 55, e.g. Northern Cassowary *Casuarius unappendiculatus*, Mimic Honeyeater *Microptilotis analogus*). Some species lived within semi-exposed habitat near forest edges and openings in the canopy (*n = 27*, e.g. White-bellied Thicket Fantail *Rhipidura leucothorax*, Metallic Starling *Aplonis metallica*). Only one species was an open habitat specialist (Stephan´s Emerald-Dove *Chalcophaps stephani*). Regarding trophic niche, the category with the largest number of species was invertivores (*n* = 33, e.g. Rufous-bellied Kookaburra *Dacelo gaudichaud*, Sepik-Ramu Shrike-thrush), followed by frugivores (*n* = 26, e.g. Victoria Crowned Pigeon *Goura victoria,* Lesser Bird-of-Paradise *Paradisaea minor*) and omnivores (*n* = 19*,* e.g. Sulphur-crested Cockatoo *Cacatua galerita*, Coconut Lorikeet *Trichoglossus haematodus*). Other trophic niches were represented by only one species each (aquatic predator: Azure Kingfisher *Ceyx azureus*, granivore: Streak-headed Mannikin *Mayrimunia tristissima*, nectarivore: Black-capped Lory *Lorius lory*, herbivore: Buff-faced Pygmy Parrot *Micropsitta pusio*, and vertivore: Ivory-billed Coucal *Centropus menbeki*). In terms of primary lifestyle, almost all

Table 1. Effect of primary and spatial predictors on bird community structure using variance partitioning multivariate analysis (PCNM). *P* = probability.

Predictor	*Explained variability %*	*Pseudo-F*	*P*
Primary predictor			
River presence	13.2	2.7	0.008
Spatial predictors			
PCO.7	20.5	2.7	0.026
PCO.3	20.5	3.0	0.004
PCO.1	17.1	2.8	0.010

species at our study site were insessorial (*n* = 72), staying on branches of trees and other raised substrates. Only seven species were terrestrial, spending the majority of their lives on the ground (e.g. Northern Cassowary, Collared Brush-turkey *Talegalla jobiensis*), three were generalists with no stable primary lifestyle (Stephan´s Emerald-Dove, Papuan Babbler *Garritornis isidorei*, Streak-headed Mannikin), and only one was an aerial specialist (Oriental Dollarbird *Eurystomus orientalis*). Functional traits for every species are presented in Appendices 1–2, and explanations of all functional traits and trait values in Appendix 3.

Community structure

The multivariate analysis (PCNM) supported our hypothesis that bird community structure would differ significantly between riparian and upland zones (Table 1). The strongest effect on trait-level response was represented by spatial predictors that described the cumulative effect of spatial autocorrelation (spatial coordinates, 21.6% of all variation), followed by the primary predictor (river presence/absence, 5.0%), and the shared fraction of both spatial and primary predictors (3.6%). The amounts of variation explained by specific predictors as well as respective significance levels and test statistic values are listed in Table 1.

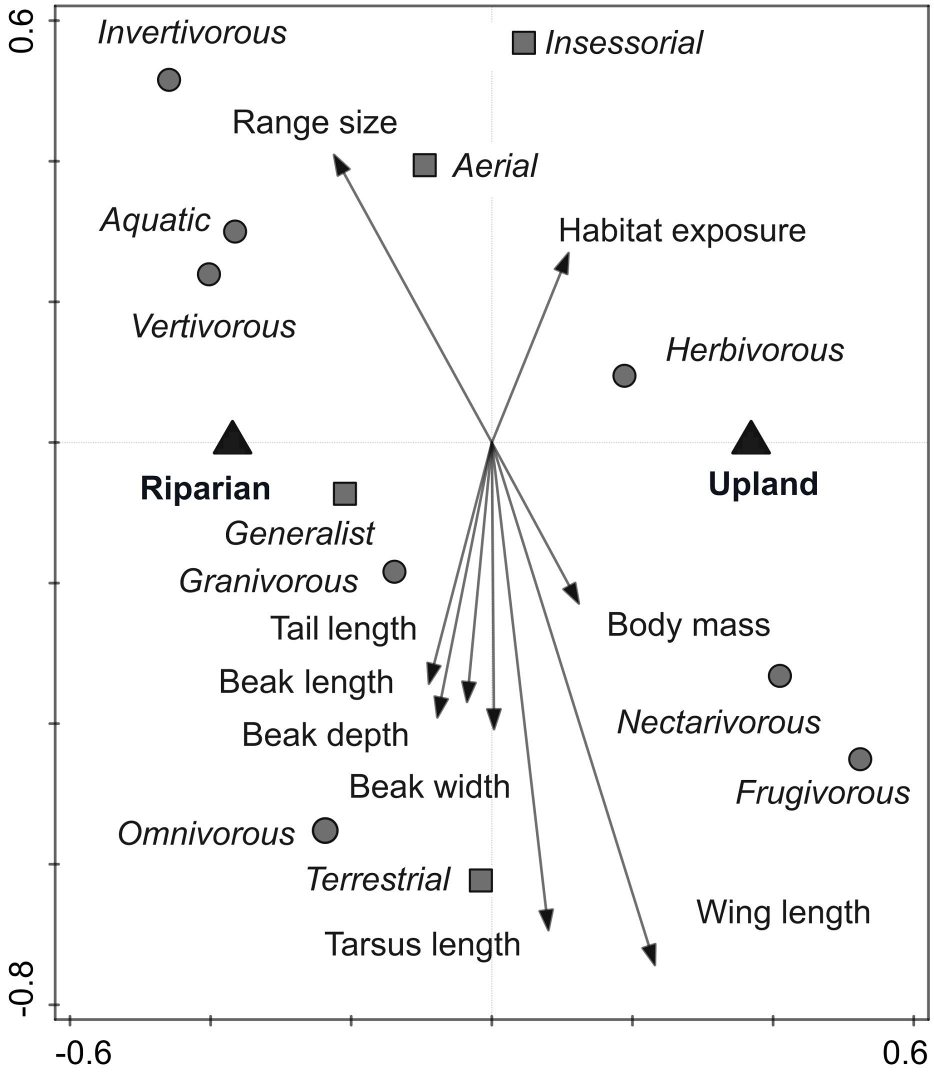

Figure 3. Projected scores for functional traits in relation to habitat type, distinguishing between riparian and upland habitats. All functional traits used are displayed. Arrows represent traits with continuous values, circles represent different trophic niches, and squares different primary lifestyles of bird species at the study site. For explanations of traits and trait values see Appendix 3.

Bird response to habitat type (riparian/upland) was visually represented by the ordination diagram output of the multivariate analysis along the first ordination axis (Figure 3). This diagram shows that some functional traits were exhibited more by birds present in riparian areas, whereas others were more typical for upland birds. We further highlight this by supplying linear regression coefficients ($\beta1$) of each trait with scores from the first ordination axis of the multivariate analysis. This way we describe whether a trait´s values were correlated with riparian ($\beta1 > 0$) or upland ($\beta1 < 0$) habitats. In terms of trophic niche, aquatic predators, vertivores and invertivores were positively correlated with river presence ($\beta1$ = 1.43, 1.56, 1.44, respectively). Granivores and omnivores also showed preference for riparian habitats ($\beta1$ = 0.22, 0.30 respectively). On the other hand, herbivores, nectarivores and frugivores all showed preference for habitats away from rivers ($\beta1$ = – 1.42, – 1.42, – 1.84, respectively). In terms of habitat exposure, species living in dense understorey preferred riparian habitats but open-habitat birds preferred uplands ($\beta1$ = – 0.39). Regarding primary lifestyle, birds most attracted to riparian habitats were generalists ($\beta1$ = 0.80). Other lifestyles, such as terrestrial, insessorial (perching) or aerial, were not correlated with either riparian or upland habitats.

Continuous traits describing body dimensions were often correlated with each other (Figure 3). Higher values of tail length, beak length and beak depth were all slightly positively correlated with river presence ($\beta1$ = 0.33, 0.2, 0.11, respectively), whereas greater wing length and tarsus length were negatively correlated with river presence ($\beta1$ = – 0.83, – 0.28, respectively). Higher body mass was also typical for birds away from the river ($\beta1$ = – 0.44). Lastly, species with greater geographic range were more abundant near rivers than sedentary species with smaller, restricted home ranges ($\beta1$ = 1.31).

Strong correlations were found between some functional traits, which is highlighted by their similar locations on the ordination diagram (Figure 3). We further support this by supplying Pearson´s coefficients of correlation (*r*) between individual traits. For example, greater geographical range was positively correlated with invertivory and vertivory in terms of trophic niche (*r* = 0.2, 0.4). Conversely, frugivory and nectarivory showed a negative correlation with greater geographical range (*r* = – 0.15, – 0.17). On the other hand, frugivory was correlated positively with greater body mass (*r* = 0.57), in contrast with invertivory and vertivory (*r* = – 0.60, – 0.51). Greater beak length and depth and tail length were positively correlated with omnivory (*r* = 0.23, 0.09). Higher habitat exposure was highly correlated with herbivory (*r* = 0.36) but negatively correlated with both omnivory and granivory (*r* = – 0.24, – 0.19), as species of these trophic niches lived in high-density habitats.

Species diversity

Using distance from observer as a random effect, we found only a marginally significant positive effect of river presence on species diversity (median non-river diversity 3.21, median river diversity 3.30, *P* = 0.063: Table 2). These results did not support our hypothesis that there would be increased diversity in riparian areas.

Table 2. Effect of independent variable on bird diversity within the study area based on a mixed-effects linear model. Random effects were represented by category of distance from observer (0–10, 11–20, 21–30, 31–40, 41–50 m). SE = Standard Error, T= *t*- value, *P* = probability.

Independent variable	*Estimate*	*SE*	*T*	*P*
River presence	0.090	0.048	1.875	0.065

Discussion

Community structure

Functional traits enhance the capability of researchers to study bird community structure response to environmental variables. Among ornithological studies in the region, the trophic guild was perhaps the functional trait most utilised and was used to examine effects of anthropogenic disturbance (Sam *et al*. 2014) or vertical stratification (Chmel *et al*. 2016). In our study, the trophic guild of birds varied significantly between riparian and upland zones.

A large assemblage of invertivores was likely to be present near a river. River presence facilitates greater availability of aquatic invertebrate prey (Uesugi & Murakami 2007), which leads to increased abundance of invertivores in riparian zones (Murakami & Nakano 2007). Invertivore river preference may also be related to vegetation structure: vegetation near rivers is subject to natural disturbances, which create edges and openings in the canopy, producing variation in vegetation height and density (Salo *et al*. 1986). Increased habitat heterogeneity has in general a positive effect on species richness of invertivorous birds (Castaño-Villa *et al*. 2014). As invertivores generally occur in mid-understorey and lower canopy (Chmel *et al*. 2016), and their food sources are not tied to presence of particular tree species, they can easily adapt to localised disturbance (Thiollay 1999).

This is in sharp contrast to frugivores and nectarivores, which showed preference for habitats away from the rivers. These birds are mostly restricted to the canopy where they seek out fruiting trees for food (e.g. Wompoo Fruit-Dove *Ptilinopus magnificus*, Lesser Bird-of-Paradise: Frith & Frith 2020). Frugivores were previously reported to be limited by the availability of fruiting trees (Robinson & Terborgh 1997) and significantly affected by disturbances (Tvardíková 2010). Anjos *et al*. (2007) found that frugivores were less abundant in riparian areas and suggested that this may be related to decreased numbers of fruiting trees near rivers. This is likely because of greater spacing between individual trees and larger canopy gaps in riparian forest (Bianchini *et al*. 2001).

Our results showed that frugivory was strongly correlated with higher body mass. Frugivorous birds at our study site included the Northern Cassowary and Blyth´s Hornbill *Rhyticeros plicatus* but also numerous species of fruit-doves *Ptilinopus* spp. and imperial-pigeons *Ducula* spp. These species were considerably larger in body mass than most invertivores at our study site. Higher body mass was also positively correlated with wing and tarsus length, as expected, as longer limbs typically correlate with higher body mass (Prange *et al*. 1979).

Tail length and beak dimensions (length, width, depth) correlated negatively with habitat exposure: it appeared that species living in dense habitats had longer tails and greater beak dimensions. This effect was mostly represented by omnivorous birds, with generalist lifestyles, that moved freely through the rainforest interior. These species have higher body mass, but they also have bigger, longer beaks adapted to foraging in multiple trophic niches: parrots and cockatoos feed on a wide range of fruits, seeds and buds (Rowley *et al.* 2020), but starlings and honeyeaters feed on nectar, fruits and invertebrates (Higgins *et al.* 2020). Longer tail-feathers may improve dexterity when foraging in various environments, acting as supports when climbing on tree trunks or branches high in the canopy (Reader *et al*. 2022). Omnivore adaptiveness when foraging for food also means that omnivores are not strictly restricted by one type of food source becoming unavailable, in contrast to frugivores. Some omnivores at our study site have also been reported to respond positively to disturbances (e.g. friarbirds and cockatoos: Higgins *et al.* 2020; Rowley *et al.* 2020), facilitating their preference for riparian zones.

In terms of geographical range, birds with greater ranges were attracted to riparian zones. Rivers function as natural corridors in the rainforest, facilitating bird dispersal (Sekercioglu 2009). The trophic guild correlated with larger home ranges was invertivores, whereas frugivore geographical ranges were smaller. Frugivores included some terrestrial birds with low dispersal capabilities (e.g. Northern Cassowary, Collared Brush-turkey). Frugivorous birds were often habitat specialists (Snow 1981), again because of the strong dependence on fruiting trees as main food sources (Robinson & Terborgh 1997). In contrast, insectivores and omnivores can make use of alternative food sources and show greater adaptability to structural changes (Castaño-Villa *et al*. 2014). As a result, invertivores are less restricted by habitat availability and therefore have greater geographical ranges.

Spatial autocorrelation

Our results showed a significant effect of spatial autocorrelation on bird community structure. This is not atypical, as many other researchers studying bird ecology in the tropics have encountered high levels of spatial autocorrelation (Lehmkuhl *et al.* 2007; Kamga *et al.* 2022). However, others neglected to include it as a covariate in community analyses and presented their findings as if no confounding effects were present (e.g. Bub *et al.* 2004; Tvardíková 2010). As spatial autocorrelation is nearly ubiquitous in ecological data, neglecting its effect may lead to misleading findings (Ewers & Didham 2006; Šmilauer & Lepš 2014). However, as we properly addressed this in our multivariate analysis, the significant effect of habitat type on bird community is free of confounding factors.

Species diversity

We found only a marginal effect of disturbances related to river presence on species diversity. Riparian habitats are often regarded as harbouring increased numbers of species compared with upland zones (Naiman *et al*. 1993; National Research Council 2002). This is not always the case. Murray & Stauffer (1995) found no differences in species richness between upland and riparian forest birds. Salo *et al*. (2005) also found no significant difference in species richness but highlighted strong differences in species turnover and community structure. This illustrates that using solely community indices for examining bird communities may lead to loss of valuable information.

Conclusions

This study is the first to compare bird communities in riparian and upland zones of a semi-continuous New Guinean rainforest. The adaptability of bird communities to structural changes related to natural disturbances in riparian zones was highlighted by a comprehensive multivariate analysis. Species from different trophic niches, such as omnivores or invertivores, were capable of exploiting the periodical food supply associated with riparian forest without relying on dense canopy cover, although other niches, such as for frugivores and nectarivores, required a relatively undisturbed vegetation cover with fruiting and flowering trees. Other functional traits were associated with different habitat types, as smaller species with larger geographical ranges living in dense forest interior preferred riparian forest in contrast to large sedentary birds of exposed canopy strata that preferred upland areas. The new information on community structure with respect to river-related disturbance could be further expanded by including additional study sites within the region to include more species and functional groups. Bird response to riparian disturbances could also be investigated on multiple elevation levels, relating to the highly diverse topography of New Guinea. The statistical methodology of this study along with the introduction of functional traits may serve as a baseline for a more expansive survey in the future.

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References

Anderson-Teixeira, K.J., Davies, S.J. & Zimmerman, J. (2015). CTFS-Forest GEO: A worldwide network monitoring forests in an era of global change. *Global Change Biology* **21**, 528–549.

Anjos, L.D., Volpato, G.H., Lopes, E.V., Serafini, P.P., Poletto, F. & Aleixo, A. (2007). The importance of riparian forest for the maintenance of bird species richness in an Atlantic Forest remnant, southern Brazil. *Revista Brasileira de Zoologia* **24**, 1078–1086.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). Fitting linear mixed-effects models using lme4. arXiv preprint, arXiv: 1406.5823. https://doi.org/10.48550/arXiv.1406.5823

Batisteli, A.F., Tanaka, M.O. & Souza, A.L. (2018). Bird functional traits respond to forest structure in riparian areas undergoing active restoration. *Diversity* **10**, 90.

Bell, H.L. (1984). A bird community of lowland rainforest in New Guinea: Foraging ecology and community structure of the avifauna. *Emu* **84**, 142–158.

Bender, I., Kissling, W.D., Böhning-Gaese, K., Hensen, I., Kühn, I., Nowak, L., Töpfer, T., Wiegand, T., Dehling, M. & Schleuning M. (2019). Projected impacts of climate change on functional diversity of frugivorous birds along a tropical elevational gradient. *Scientific Reports* **9**, 17708.

Bianchini. E., Pimenta. J.A. & Dos Santos, F.A. (2001). Spatial and temporal variation in the canopy cover in a tropical semi-deciduous forest. *Brazilian Archives of Biology and Technology* **44**, 269–276.

Boisgontier, M.P. & Cheval, B. (2016). The anova to mixed model transition. *Neuroscience & Biobehavioral Reviews* **68**, 1004–1005.

Bub, B.R., Flaspohler, D.J. & Huckins, C.J. (2004). Riparian and upland breeding bird assemblages along headwater streams in Michigan's Upper Peninsula. *Journal of Wildlife Management* **68**, 383–392.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48**, 1079–1087.

Carlisle, J.D. & McDonald, T.L. (2015). Rdistance Tutorial for Beginners. Microsoft R Application Network. Available online: https://mran.microsoft.com/snapshot/2015-06-15/web/packages/Rdistance/vignettes/Rdistance_BeginnerTutorial.pdf

Castaño-Villa, G.J., Ramos-Valencia, S.A. & Fontúrbel, F.E. (2014). Fine-scale habitat structure complexity determines insectivorous bird diversity in a tropical forest. *Acta Oecologica* **61**, 19–23.

Cernansky, R. (2017). Biodiversity moves beyond counting species. *Nature* **546**, 22–24.

Chmel, K., Riegert, J., Paul, L. & Novotný, V. (2016). Vertical stratification of an avian community in New Guinean tropical rainforest. *Population Ecology* **58**, 535–547.

Da Silva, J.M.C. & Vickery, P.D. (2002). Birds. In: Perrow, M.R. & Davy, A.J. (Eds). *Handbook of Ecological Restoration*, pp. 376–388. Cambridge University Press, Cambridge, UK.

Esri Inc. (2020). *ArcGIS Pro version 2.5.* Esri Inc., Redlands, California, USA.

Ewers, R.M. & Didham, R.K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* **81**, 117–142.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Reviews of Ecology, Evolution and Systematics* **34**, 487–515.

Frith, C. & Frith, D. (2020). Lesser Bird-of-Paradise (*Paradisaea minor*), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (Eds). *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, USA. Available online: https://doi.org/10.2173/bow.lbopar1.01

Gałecki, A. & Burzykowski, T. (2013). Linear mixed effects model. In: Gałecki, A. & Burzykowski, T. (Eds). *Linear Mixed Effects Models Using R*, pp. 245–273. Springer, New York, USA

Gardali, T., Holmes, A.L., Small, S.L., Nur, N., Geupel, G.R. & Golet, G.H. (2006). Abundance patterns of landbirds in restored and remnant riparian forests on the Sacramento River, California, USA. *Conservation Biology* **14**, 391–403.

Gill, F., Donsker, D. & Rasmussen, P. (Eds) (2023). *IOC World Bird List (v13.1).* doi:10.14344/IOC.ML.13.1.

Helms, IV., J.A., Woerner, C.R., Fawzi, N.I. & MacDonald, A. (2018). Rapid response of bird communities to small-scale reforestation in Indonesian Borneo. *Tropical Conservation Science* **11**, 1940082918769460.

Higgins, P.J., Christidis, L. & Ford, H. (2020). Meyer's Friarbird (*Philemon meyeri*), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (Eds). *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, USA. Available online: https://doi.org/10.2173/bow.meyfri1.01

Hill, J.K. & Hamer, K.C. (2004). Determining impacts of habitat modification on diversity of tropical forest fauna: The importance of spatial scale. *Journal of Applied Ecology* **41**, 744–754.

Hinojosa-Huerta, O., Nagler, P.L., Carrillo-Guererro, Y.K. & Glenn, E.P. (2013). Effects of drought on birds and riparian vegetation in the Colorado River Delta, Mexico. *Ecological Engineering* **51**, 275–281.

Kamga, S.M., Tamungang, S.A. & Awa, II., T. (2022). The importance of forest elephants for vegetation structure modification and its influence on the bird community of mid-elevation forest on Mount Cameroon, West-Central Africa. *Diversity* **14**, 227.

Kleyer, M., Dray, S., de Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W. & Lavorel, S. (2012). Assessing species and community functional responses to environmental gradients: Which multivariate methods? *Journal of Vegetation Science* **23**, 805–821.

Legendre, P. & Legendre, L. (2012). *Numerical Ecology*. Elsevier, Amsterdam.

Lehmkuhl, J.F., Burger, E.D., Drew, E.K., Lindsey, J.P., Haggard, M. & Woodruff, K.Z. (2007). Breeding birds in riparian and upland dry forests of the Cascade Range. *Journal of Wildlife Management* **71**, 2632–2643.

Maicher, V., Delabye, S. & Murkwe, M. (2020). Effects of disturbances by forest elephants on diversity of trees and insects in tropical rainforests on Mount Cameroon. *Scientific Reports* **10**, 10–11.

Marques, T.A., Thomas, L., Fancy, S.G. & Buckland S.T. (2007). Improving estimates of bird density using multiple-covariate distance sampling. *Auk* **124**, 1229–1243.

Marrot, P., Garant, D. & Charmantier, A. (2015). Spatial autocorrelation in fitness affects the estimation of natural selection in the wild. *Methods in Ecology and Evolution* **6**, 1474–1483.

Martin, T.E., Nightingale, J. & Simcox, W. (2017). Variability in the effectiveness of two ornithological survey methods between tropical forest ecosystems. *PLoS One* **12**, e0169786.

McAlpine, J.R., Keig, G. & Falls, R. (1983). *Climate of Papua New Guinea*. Commonwealth Scientific and Industrial Research Organization in association with Australian National University Press, Canberra.

McDonald, T., Nielson, R. & Carlisle, J. (2015). *Package 'Rdistance'*. Microsoft R Application Network.

Melick, D.R. & Ashton, D.H. (1991). The effects of natural disturbances on warm temperate rainforests in southeastern Australia. *Australian Journal of Botany* **39**, 1–30.

Miller, D.L., Rexstad, E. & Thomas, L. (2017). Distance sampling in R. *BioRxiv* 063891.

Mitchell, S.L., Edwards, D.P., Bernard, H., Coomes, D., Jucker, T., Davies, Z.G. & Struebig, M.J. (2018). Riparian reserves help protect forest bird communities in oil palm dominated landscapes. *Journal of Applied Ecology* **55**, 2744–2755.

Mulvaney, J.M. & Cherry, M.I. (2020). The effectiveness of point counts and mistnetting in surveying Afrotemperate forest bird community structure in South Africa. *Emu - Austral Ornithology* **120**, 103–113.

Murakami, M. & Nakano, S. (2002). Indirect effect of aquatic insect emergence on a terrestrial insect population through by bird's predation. *Ecology Letters* **5**, 333–337.

Murray, N.L. & Stauffer, F. (1995). Nongame bird use of habitat in central Appalachian riparian forests. *Journal of Wildlife Management* **59**, 78–88.

Naiman, R.J., Decamps, H. & Pollock, M. (1993). The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* **3**, 209–212.

National Research Council (2002). *Riparian Areas: Functions and Strategies for Management*. National Academies Press, Washington DC, USA.

Newbold, T., Scharlemann, J.P., Butchart, S.H., Şekercioğlu, Ç.H., Joppa, L., Alkemade, R. & Purves, D.W. (2014). Functional traits, land-use change and the structure of present and future bird communities in tropical forests. *Global Ecology and Biogeography* **23**, 1073–1084.

Ocampo, D. & Londoño, G.A. (2015). Tropical montane birds have increased nesting success on small river islands. *Auk* **132**, 1–10.

Palmer, G.C. & Bennett, A.F. (2006). Riparian zones provide for distinct bird assemblages in forest mosaics of south-east Australia. *Biological Conservation* **130**, 447–457.

Prange, H.D., Anderson, J.F. & Rahn, H. (1979). Scaling of skeletal mass to body mass in birds and mammals. *American Naturalist* **113**, 103–122.

R Core Team (2019). *R*: *A Language and Environment for Statistical Computing, version 3.5.1*. R Foundation for Statistical Computing, Vienna.

Reader, L.L., Carrier, D.R., Goller, F., Isaacs, M.R., Moore, C.A., Barnes, C.J. & Lee, D.V. (2022). Climbing parrots achieve pitch stability using forces and free moments produced by axial-appendicular couples. *Journal of Experimental Biology* **225**, 242305.

Remsen, Jr., J.V. & Parker, III., T.A. (1983). Contribution of river-created habitats to bird species richness in Amazonia. *Biotropica* **15**, 223–231.

Richter, R. & Stromberg, J.C. (2005). Soil seed banks of two montane riparian areas: Implications for restoration. *Biodiversity & Conservation* **14**, 993–1016.

Robinson, S.K. & Terborgh, J. (1997). Bird community dynamics along primary successional gradients of an Amazonian whitewater river. *Ornithological Monographs* **48**, 641–672.

Rodewald, P.G. & Matthews, S.N. (2005). Landbird use of riparian and upland forest stopover habitats in an urban landscape. *Condor* **107**, 259–268.

Rowley I., Kirwan, G.M. & Boesman, P.F.D. (2020). Sulphur-crested Cockatoo (*Cacatua galerita*), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (Eds). *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, USA. Available online: https://doi.org/10.2173/bow.yeccoc1.01

Salo, J., Kalliola, R., Häkkinen, I., Mäkinen, Y., Niemelä, P., Puhakka, M. & Coley, P.D. (1986). River dynamics and the diversity of Amazon lowland forest. *Nature* **322**, 254–258.

Sam, K., Koane, B. & Jeppy, S. (2017). Diet of land birds along an elevational gradient in Papua New Guinea. *Scientific Reports* **7**, 44018.

Sam, K., Koane, B., Jeppy, S. & Novotny, V. (2014). Effect of forest fragmentation on bird species richness in Papua New Guinea. *Journal of Field Ornithology* **85**, 152–167.

Sekercioglu, C.H. (2009). Tropical ecology: Riparian corridors connect fragmented forest bird populations. *Current Biology* **19**, 210–213.

Sekercioglu, C.H., Loarie, S.R., Oviedo-Brenes, F., Mendenhall, C.D., Daily, G.C. & Ehrlich, P.R. (2015). Tropical countryside riparian corridors provide critical habitat and connectivity for seed-dispersing forest birds in a fragmented landscape. *Journal of Ornithology* **156**, 343–353.

Shannon, C.E. & Weaver, W. (1949). *The Mathematical Theory of Communication.* University of Illinois Press, Urbana, Illinois, USA.

Shearman, P.L., Ash, J. & Mackey, B. (2009). Forest conversion and degradation in Papua New Guinea 1972–2002. *Biotropica* **41**, 379–390.

Šmilauer, P. & Lepš, J. (2014). *Multivariate Analysis of Ecological Data Using CANOCO 5.* Cambridge University Press, Cambridge, UK.

Snow, D.W. (1981). Tropical frugivorous birds and their food plants: A world survey. *Biotropica* **13**, 1–14.

Sodhi, N.S., Koh, L.P. & Brook, B. (2004). Southeast Asian biodiversity: An impending disaster. *Trends in Ecology and Evolution* **19**, 654–660.

Thiollay, J.M. (1999). Responses of an avian community to rain forest degradation. *Biodiversity and Conservation* **8**, 513–534.

Thompson, W.L. (2002). Towards reliable bird surveys: Accounting for individuals present but not detected. *Auk* **119**, 18–25.

Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., Sayol, F., Neate-Clegg, M.H.C., Alioravainen, N., Weeks, T.L., Barber, R.A., Walkden, P.A., MacGregor, H.E.A., Jones, S.E.I., Vincent, C., Phillips, A.G., Marples, N.M., Montaño-Centellas, F.A., Leandro-Silva, V., Claramunt, S. & Schleuning, M. (2022). AVONET: Morphological, ecological, and geographical data for all birds. *Ecology Letters* **25**, 581–597.

Tvardíková, K. (2010). Bird abundances in primary and secondary growths in Papua New Guinea: A preliminary assessment. *Tropical Conservation Science* **3**, 373–388.

Uesugi, A. & Murakami, M. (2007). Do seasonally fluctuating aquatic subsidies influence the distribution pattern of birds between riparian and upland forests? *Ecological Research* **22**, 274–281.

Vandewalle, M., de Bello, F., Berg, M.P., Bolger, T., Dolédec, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P.A., Lavorel, S., da Silva, P., Moretti, M., Niemelä, J., Santos, P., Sattler, T., Sousa, J., Sykes, M., Vanbergen, A. & Woodcock, B. (2010). Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation* **19**, 2921–2947.

Volpato, G.H., Lopes, E.V. & Mendonça, L.B. (2009). The use of the point count method for bird survey in the Atlantic Forest. *Zoologia (Curitiba)* **26**, 74–78.

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Appendix 1. Bird species used in analyses in this study: maximum number of individuals detected at one study plot, and information on some functional traits (habitat density, trophic niche, and primary lifestyle). Information was taken from the AVONET dataset as introduced by Tobias *et al*. (2022). Specifications of the meaning of different functional traits and their values are available in Appendix 3. Habitat density: 1 = dense habitats, 2 = medium-density habitats, 3 = open, exposed habitats; trophic niche: A = aquatic predator, F = frugivore, G = granivore, H = herbivore, terrestrial, I = invertivore, N = nectarivore, O = omnivore, V = vertivore; primary lifestyle: A = aerial, G = generalist, I = insessorial, T = terrestrial.

Species	*Family*	*Max. abundance*	*Habitat density*	*Trophic niche*	*Primary lifestyle*
Northern Cassowary *Casuarius unappendiculatus*	Casuariidae	1	1	F	T
Collared Brush-turkey *Talegalla jobiensis*	Megapodiidae	5	1	O	T
Ivory-billed Coucal *Centropus menbeki*	Cuculidae	1	2	V	T
Pacific Koel *Eudynamys orientalis*	Cuculidae	2	2	F	I
Little Bronze-Cuckoo *Chrysococcyx minutillus*	Cuculidae	1	1	I	I
Brush Cuckoo *Cacomantis variolosus*	Cuculidae	3	1	I	I
Amboyna Cuckoo-Dove *Macropygia amboinensis*	Columbidae	1	1	F	I
Great Cuckoo-Dove *Reinwardtoena reinwardti*	Columbidae	1	1	F	I
Stephan’s Emerald-Dove *Chalcophaps stephani*	Columbidae	1	3	O	G
Cinnamon Ground Dove *Gallicolumba rufigula*	Columbidae	2	1	O	T
Victoria Crowned Pigeon *Goura victoria*	Columbidae	2	2	F	T
Wompoo Fruit-Dove *Ptilinopus magnificus*	Columbidae	3	2	F	I
Pink-spotted Fruit-Dove *Ptilinopus perlatus*	Columbidae	1	2	F	I
Superb Fruit-Dove *Ptilinopus superbus*	Columbidae	3	2	F	I
Coroneted Fruit-Dove *Ptilinopus coronulatus*	Columbidae	2	2	F	I
Beautiful Fruit-Dove *Ptilinopus pulchellus*	Columbidae	4	2	F	I
Orange-bellied Fruit-Dove *Ptilinopus iozonus*	Columbidae	3	2	F	I
Purple-tailed Imperial-Pigeon *Ducula rufigaster*	Columbidae	2	2	F	I
Pinon’s Imperial-Pigeon *Ducula pinon*	Columbidae	2	2	F	I
Zoe’s Imperial-Pigeon *Ducula zoeae*	Columbidae	3	2	F	I
Papuan Mountain Pigeon *Gymnophaps albertisii*	Columbidae	6	1	F	I
Blyth’s Hornbill *Rhyticeros plicatus*	Bucerotidae	8	1	F	I

Appendix 1 continued

Species	*Family*	*Max. abundance*	*Habitat density*	*Trophic niche*	*Primary lifestyle*
Oriental Dollarbird *Eurystomus orientalis*	Coraciidae	1	2	I	A
Hook-billed Kingfisher *Melidora macrorrhina*	Alcedinidae	1	1	I	I
Common Paradise-Kingfisher *Tanysiptera galatea*	Alcedinidae	5	1	I	I
Rufous-bellied Kookaburra *Dacelo gaudichaud*	Alcedininae	6	1	I	I
Yellow-billed Kingfisher *Syma torotoro*	Alcedinidae	2	1	I	I
Papuan Dwarf Kingfisher *Ceyx solitarius*	Alcedininae	4	1	I	I
Azure Kingfisher *Ceyx azureus*	Alcedininae	2	2	A	I
Palm Cockatoo *Probosciger aterrimus*	Cacatuidae	3	2	O	I
Sulphur-crested Cockatoo *Cacatua galerita*	Cacatuidae	4	1	O	I
Buff-faced Pygmy Parrot *Micropsitta pusio*	Psittaculidae	2	2	H	I
Eclectus Parrot *Eclectus roratus*	Psittaculidae	4	1	O	I
Red-cheeked Parrot *Geoffroyus geoffroyi*	Psittaculidae	6	1	O	I
Black-capped Lory *Lorius lory*	Psittaculidae	4	1	N	I
Coconut Lorikeet *Trichoglossus haematodus*	Psittaculidae	6	1	O	I
Edward's Fig-Parrot *Psittaculirostris edwardsii*	Psittaculidae	4	1	F	I
Tan-capped Catbird *Ailuroedos geislerorum*	Ptilonorhynchidae	3	1	O	I
Long-billed Honeyeater *Melilestes megarhynchus*	Meliphagidae	2	1	O	I
Plain Honeyeater *Pycnopygius ixoides*	Meliphagidae	3	1	O	I
Meyer's Friarbird *Philemon meyeri*	Meliphagidae	2	1	O	I
Helmeted Friarbird *Philemon buceroides*	Meliphagidae	2	2	O	I
Tawny-breasted Honeyeater *Xanthotis flaviventer*	Meliphagidae	2	1	I	I
Puff-backed Honeyeater *Meliphaga aruensis*	Meliphagidae	2	1	O	I
Mimic Honeyeater *Microptilotis analogus*	Meliphagidae	6	1	O	I
Rusty Mouse-warbler *Origma murina*	Acanthizidae	2	1	I	T

Appendix 1 continued

Species	*Family*	*Max. abundance*	*Habitat density*	*Trophic niche*	*Primary lifestyle*
Large-billed Gerygone *Gerygone magnirostris*	Acanthizidae	4	2	I	I
Yellow-bellied Gerygone *Gerygone chrysogaster*	Acanthizidae	3	1	I	I
Green-backed Gerygone *Gerygone chloronota*	Acanthizidae	2	1	I	I
Fairy Gerygone *Gerygone palpebrosa*	Acanthizidae	2	1	I	I
Papuan Babbler *Garritornis isidorei*	Pomatostomidae	2	1	I	G
Black Berrypecker *Melanocharis nigra*	Melanocharitidae	2	1	F	I
Yellow-bellied Longbill *Toxorhamphus novaeguineae*	Melanocharitidae	2	1	O	I
Blue Jewel-babbler *Ptilorrhoa caerulescens*	Cinclosomatidae	2	1	I	T
Yellow-breasted Boatbill *Machaerirhynchus flaviventer*	Machaerirhynchidae	2	1	I	I
Black Butcherbird *Melloria quoyi*	Artamidae	2	1	I	I
Boyer’s Cuckoo-shrike *Coracina boyeri*	Campephagidae	2	1	F	I
Black-browed Triller *Lalage atrovirens*	Campephagidae	2	2	F	I
Grey Whistler *Pachycephala simplex*	Pachycephalidae	4	1	I	I
Rusty Pitohui *Pseudorectes ferrugineus*	Pachycephalidae	4	1	O	I
Sepik-Ramu Shrike-thrush *Colluricincla tappenbecki*	Pachycephalidae	4	1	I	I
Northern Variable Pitohui *Pitohui kirhocephalus*	Oriolidae	9	2	I	I
Brown Oriole *Oriolus szalayi*	Oriolidae	2	2	O	I
Spangled Drongo *Dicrurus bracteatus*	Dicruridae	4	1	I	I
Northern Fantail *Rhipidura rufiventris*	Rhipiduridae	2	2	I	I
Sooty Thicket Fantail *Rhipidura threnothorax*	Rhipiduridae	4	1	I	I
White-bellied Thicket Fantail *Rhipidura leucothorax*	Rhipiduridae	2	2	I	I
Rufous-backed Fantail *Rhipidura rufidorsa*	Rhipiduridae	2	1	I	I
Spot-winged Monarch *Symposiachrus guttula*	Monarchidae	2	1	I	I
Hooded Monarch *Symposiachrus manadensis*	Monarchidae	2	1	I	I

Appendix 1 continued

Species	*Family*	*Max. abundance*	*Habitat density*	*Trophic niche*	*Primary lifestyle*
Rufous Monarch *Symposiachrus rubiensis*	Monarchidae	2	1	I	I
Golden Monarch *Carterornis chrysomela*	Monarchidae	3	1	I	I
Ochre-collared Monarch *Arses insularis*	Monarchidae	3	1	I	I
Shining Flycatcher *Myiagra alecto*	Monarchidae	3	2	I	I
Grey Crow *Corvus tristis*	Corvidae	3	1	F	I
King Bird-of-Paradise *Cicinnurus regius*	Paradisaeidae	2	1	O	I
Lesser Bird-of-Paradise *Paradisaea minor*	Paradisaeidae	5	1	F	I
Black-sided Robin *Poecilodryas hypoleuca*	Petroicidae	4	1	I	I
Metallic Starling *Aplonis metallica*	Sturnidae	7	2	F	I
Singing Starling *Aplonis cantoroides*	Sturnidae	2	2	F	I
Yellow-faced Myna *Mino dumontii*	Sturnidae	7	1	F	I
Red-capped Flowerpecker *Dicaeum geelvinkianum*	Dicaeidae	2	1	F	I
Streak-headed Mannikin *Mayrimunia tristissima*	Estrildidae	4	2	G	G

Appendix 2. The remaining functional traits of each bird species used in our analyses. Information was taken from the AVONET dataset, as introduced by Tobias *et al*. (2022). Descriptions of different functional traits used, and their values, are available in Appendix 3. For range sizes above 1 million km^2, the numbers are rounded up to the closest million and exponential notation is used.

Species	*Beak (mm)*			*Tarsus length (mm)*	*Wing length (mm)*	*Tail length (mm)*	*Body mass (g)*	*Range size (km^2)*
	Length	*Width*	*Depth*					
Northern Cassowary	88.1	14.3	23.2	303.4	264.5	273.5	46073.85	185351
Collared Brush-turkey	37.9	11.2	19.1	84.7	286.2	181.2	1478.81	209938
Ivory-billed Coucal	49.8	11	21.5	58.3	218.2	347	519	645860
Pacific Koel	33.9	10	11.1	37.4	209.9	206	194.92	3E + 06
Little Bronze-Cuckoo	18.8	5.1	4.7	14.7	93.2	59.6	18.6	3E + 06
Brush Cuckoo	20.5	5.3	5.4	16.3	115.4	112.9	35.75	4E + 06
Amboyna Cuckoo-Dove	21	3.5	4.8	22.8	171.9	190.6	237	1E + 06
Great Cuckoo-Dove	23.6	4.7	5.4	32.2	88.1	90	49	399425
Stephan’s Emerald-Dove	23.1	4.8	5.7	24.6	200.2	148.2	259	535761
Cinnamon Ground Dove		18.8	2.6	3.7	31.3	129.8	75.2	130
Victoria Crowned Pigeon	12.1	3.1	3	16.8	52.3	38	7.4	969224
Wompoo Fruit-Dove	15.7	3.7	3.6	19.7	117	63.8	76.6	670309
Pink-spotted Fruit-Dove	16.1	4.2	4.2	21.6	117.8	51.8	114	674306
Superb Fruit-Dove	24	5.7	5.7	27.4	156.8	84.2	210	673225
Coroneted Fruit-Dove	29.1	8.3	9.4	36.2	134.1	109.5	93.91	614817
Beautiful Fruit-Dove	14	3.4	3.1	18.5	95.8	57	53.9	26140
Orange-bellied Fruit-Dove	24.2	14.1	20.6	15.7	105.8	57	118	99152
Purple-tailed Imperial-Pigeon	36.1	9.1	8	34.6	259.4	141.6	756	635132
Pinon’s Imperial-Pigeon	34.4	10.3	11.7	23.6	150	120.2	85.53	2E + 06
Zoe’s Imperial-Pigeon	27.8	6.3	5.9	31	196.6	109	436	670937
Papuan Mountain Pigeon	45.9	8.1	9	90.2	350.5	258.2	2384	116530
Blyth’s Hornbill	15.4	5	3.9	14.6	81.6	82	12	31219
Oriental Dollarbird	40	19.4	29.7	21.6	228.2	114.6	480.76	51684
Hook-billed Kingfisher	16.4	8.2	3.5	14.9	58.2	51.9	10.32	708933
Common Paradise-Kingfisher	16.5	5.1	4.6	17.6	79	71.5	16.4	657660
Rufous-bellied Kookaburra	15.3	3.7	3.6	22.4	59.3	35.3	15	531992
Yellow-billed Kingfisher	17.3	4.9	3.9	22.8	80.8	93.4	17.6	594363
Papuan Dwarf Kingfisher	49	6.6	8.6	10.3	74	35.2	34.9	3E + 06

Appendix 2 continued

Species	*Beak (mm)*			*Tarsus length (mm)*	*Wing length (mm)*	*Tail length (mm)*	*Body mass (g)*	*Range size (km^2)*
	Length	*Width*	*Depth*					
Azure Kingfisher	16.4	5.1	4.5	17.9	72	55.7	15.6	651592
Palm Cockatoo	30.7	8.2	9	33.8	113.9	100	72	243662
Sulphur-crested Cockatoo	49.3	22.4	44.3	28.5	347.3	198.4	720.43	4E + 06
Buff-faced Pygmy Parrot	43.2	4.9	5.9	25.3	99.4	77.5	43.76	565759
Eclectus Parrot	31	6	6.1	32	219.8	127.8	568	706706
Red-cheeked Parrot	30.6	5	7	33.3	111.4	114.2	70	561084
Black-capped Lory	17.8	5	4.9	19.9	96.4	71.4	33	296185
Coconut Lorikeet	36.6	10.5	11.6	17.5	104.3	236	50	702147
Edward’s Fig-Parrot	90.9	27.6	84.4	29.5	344.2	229.2	841	716105
Tan-capped Catbird	29	9	12.3	37.9	129.6	89	138	374655
Long-billed Honeyeater	13.7	3.6	4.1	15.6	62.2	43.1	14.16	458524
Plain Honeyeater	17.1	4.2	4	20.7	129	68.8	118	2E + 06
Meyer’s Friarbird	38.9	11.2	11.5	44.5	178.4	116.3	207.93	273510
Helmeted Friarbird	15.4	3.9	5.1	15.2	70	55	17.4	93201
Tawny-breasted Honeyeater	28.2	4.1	3.9	16	64	38.3	11.78	463595
Puff-backed Honeyeater	49.3	19.5	16.5	20.3	118.2	86.8	97	654694
Mimic Honeyeater	19.3	3.3	4.3	20.3	87	69.8	26.2	665428
Rusty Mouse-warbler	50.8	13.1	16.8	34	160.6	116.6	142	554776
Large-billed Gerygone	12.7	3.4	3.1	15.7	53	41	8	557754
Yellow-bellied Gerygone	11.9	2.9	2.9	16.3	51.5	35.2	6.6	1E + 06
Green-backed Gerygone	24	11.4	17.5	15.7	147.6	76	164	793408
Fairy Gerygone	12.3	3.2	3	16.9	54.6	40	6.8	1E + 06
Papuan Babbler	32	11.8	13.4	16.8	186.2	98	143.02	1E + 07
Black Berrypecker	31.6	13.1	21.4	24.2	163	88	176.89	663810
Yellow-bellied Longbill	16.6	5.3	4.5	17.6	84.1	73.8	22.5	445281
Blue Jewel-babbler	15.4	3.6	3.6	17.2	105.6	59.4	70	339387
Yellow-breasted Boatbill	11	5.8	6.6	13.2	49.4	38.4	8.8	434282
Black Butcherbird	65	19.2	24	56.4	324.7	234.4	635	693202
Boyer’s Cuckoo-shrike	23	5.3	6.6	25.8	93.1	74.1	32.34	1E + 06

Appendix 2 continued

Species	*Beak (mm)*			*Tarsus length (mm)*	*Wing length (mm)*	*Tail length (mm)*	*Body mass (g)*	*Range size (km²)*
	Length	*Width*	*Depth*					
Black-browed Triller	18.8	5.1	4.7	14.7	93.2	59.6	18.6	3E + 06
Grey Whistler	19.8	5.9	4.7	19.3	86.4	72.4	23.58	1E + 06
Rusty Pitohui	17.6	5.4	5.2	17.4	80.4	59.4	18	419659
Sepik-Ramu Shrike-thrush	26.3	5.2	5.8	28	102.6	37.3	51.63	479514
Northern Variable Pitohui	43.1	6.3	10	36.6	147.6	127.7	108.64	1E + 06
Brown Oriole	31	8.5	10.4	35.5	151.7	74.2	217	640180
Spangled Drongo	10.6	3.2	3.5	13.4	55.9	32.4	6.8	535024
Northern Fantail	18.2	5.3	4.1	20.7	81.5	89.2	17.6	565344
Sooty Thicket Fantail	12.3	4	3.2	16.2	63.8	69.8	9.8	489139
White-bellied Thicket Fantail	18.3	3.3	4.1	22	82.4	69.4	27.58	459537
Rufous-backed Fantail	25.6	4.8	7.1	25.9	238.2	294.8	275	656098
Spot-winged Monarch	40.2	10.4	11.2	14.1	79	60.2	37.7	650715
Hooded Monarch	19.3	6.3	5.3	19.4	95	81.1	27.3	243647
Rufous Monarch	180.2	45.2	74.6	56.5	382.7	246.2	1703.76	754092
Golden Monarch	20.5	5.3	5.4	16.3	115.4	112.9	35.75	4E + 06
Ochre-collared Monarch	16.8	5.3	4.1	17.6	78.6	67.9	19.3	171996
Shining Flycatcher	21.9	3	4.1	23.2	81.1	64.3	21.57	636133
Grey Crow	22.7	7.7	8	22.3	126.9	91	66.4	604477
King Bird-of-Paradise	38.3	6.1	6	8.3	52.1	20.8	21.32	687105
Lesser Bird-of-Paradise	34.5	8.9	9.9	25.3	139.2	110.7	95.2	680369
Black-sided Robin	30.9	4.3	6.3	25	109.4	90.9	52	466261
Metallic Starling	23.1	6	7.2	22.5	107.6	97.4	56.49	767162
Singing Starling	23.4	5.5	7.1	23	97.5	69.8	55.73	822754
Yellow-faced Myna	9.7	6.7	10.2	8.8	61.3	26.5	14	290279
Red-capped Flowerpecker	54.4	18.4	18.8	17.7	130.2	91.9	143	671238
Streak-headed Mannikin	20.7	2.6	3.8	24.8	136	84.4	128.98	866814

Appendix 3. (a) Functional traits used in our analyses, unit specifications and detailed description; information was taken from the AVONET dataset legend, as introduced by Tobias *et al*. (2020). (b) Measurements.

(a) Functional traits

Functional trait	*Description*
Habitat density	1 = Dense habitats. Species primarily lives in the lower or middle storey of forest, or in dense thickets, dense shrubland etc. 2 = Semi-exposed habitats. Species primarily lives in open shrubland, scattered bushes, parkland, low dry or deciduous forest, thorn forest. 3 = Open habitats. Species primarily lives in desert, grassland, open water, low shrubs, rocky habitats, seashores, cities. Also applies to species living mainly on top of forest canopy (i.e. mostly in the open).
Trophic niche	Frugivore = species obtaining ≥60% of food resources from fruit. Granivore = species obtaining ≥60% of food resources from seeds or nuts. Nectarivore = species obtaining ≥60% of food resources from nectar. Herbivore = species obtaining ≥60% of food resources from other plant materials in non-aquatic systems, including leaves, buds, whole flowers etc. Invertivore = species obtaining ≥60% of food resources from invertebrates in terrestrial systems, including insects, worms, arachnids, etc. Vertivore = species obtaining ≥60% of food resources from vertebrate animals in terrestrial systems, including mammals, birds, reptiles etc. Aquatic Predator = species obtaining ≥60% of food resources from vertebrate and invertebrate animals in aquatic systems, including fish, crustaceans, molluscs, etc.
Primary lifestyle	Aerial = species spends much of the time in flight, and hunts or forages predominantly on the wing. Terrestrial = species spends majority of the time on the ground, where it obtains food while either walking or hopping (note this includes species that also wade in water with their body raised above the water). Insessorial = species spends much of the time perching above ground, either in branches of trees and other vegetation (i.e. arboreal), or on other raised substrates including rocks, buildings, posts and wires. Generalist = species has no primary lifestyle because it spends time in different lifestyle classes.

(b) Measurements

Measurement	*Description*
Beak length (mm)	Length from anterior edge of nostrils to tip of beak
Beak width (mm)	Width of beak at anterior edge of nostrils
Beak depth (mm)	Depth of beak at anterior edge of nostrils
Tarsus length (mm)	Length of tarsus from posterior notch between tibia and tarsus, to end of last scale of acrotarsium (at bend of foot)
Wing length (mm)	Length from carpal joint (bend of wing) to tip of longest primary on unflattened wing
Tail length (mm)	Distance between tip of longest rectrix and point at which the two central rectrices protrude from skin, typically measured using a ruler inserted between the two central rectrices
Body mass (g)	Body mass given as species average (incorporating both male and female body mass)
Range size (km^2)	Total area of mapped range of the species (not the extent of occurrence).